

## UPSTREAM AND DOWNSTREAM CAPTURE DURING SUSPENSION FEEDING BY *OLIGOMETRA SERRIPINNA* (ECHINODERMATA: CRINOIDEA) UNDER SURGE CONDITIONS

NICHOLAS D. HOLLAND, ALEXANDER B. LEONARD, AND J. RUDI STRICKLER<sup>1</sup>

*Marine Biology Research Division, Scripps Institution of Oceanography, La Jolla, California 92093 and*  
<sup>1</sup>*Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543*

### ABSTRACT

The crinoid *Oligometra serripinna* is a suspension feeder that usually experiences unidirectional tidal currents from which it extracts food particles by downstream capture (*i.e.*, while the food grooves face downcurrent). However, near slack tide, wave surge may cause brief current reversals, each lasting about 2 s at roughly 10 s intervals. To test if a crinoid can engage in upstream capture (*i.e.*, while the food grooves face upcurrent) during brief current reversals, we approximated these surge conditions in a laboratory flume. In the laboratory, as in the field, the crinoid oriented its food grooves downstream with respect to the predominant current, and the body posture did not change during the brief intervals of reversed flow. Brine shrimp cysts were added to the flume, and video recordings were made of the crinoid capturing these particles. Under surge conditions, the crinoid (1) captured 16.2% of the approaching particles while its food grooves faced downstream and (2) captured 8.0% of the approaching particles while its food grooves faced upstream. Thus *O. serripinna* used its filter both for upstream capture and for downstream capture, although the former was only about half as efficient as the latter.

### INTRODUCTION

Many suspension feeding animals use a portion of their body as a filter to capture particles from the passing water. The filter parts that capture and transport the particles may be oriented toward the current (*i.e.*, upstream capture, as in bivalves) or away from the current (*i.e.*, downstream capture, as in entoprocts). Although these definitions work well for many filter feeders, there is some question as to whether crinoids, which are generally considered downstream capturers (Magnus, 1967; Meyer, 1979, 1982; Holland *et al.*, 1986), might sometimes function as upstream capturers. In some crinoids, an animal may orient some parts of its filter upstream and other parts downstream (*e.g.*, in the cone posture and in the partial arm fan described by La Touche, 1978, and by Byrne and Fontaine, 1981). It has been implied but not clearly shown that such crinoids can engage in upstream and downstream capture simultaneously. Furthermore, in another crinoid (*Oligometra serripinna*), the filter is oriented downstream in the unidirectional tidal current that predominates in the field. However, at slack tide, wave surge causes periodic reversals in the current direction (Leonard *et al.*, 1987). During each reversal, *O. serripinna* does not change its body posture. Thus the filter is oriented upstream. The present note (1) demon-

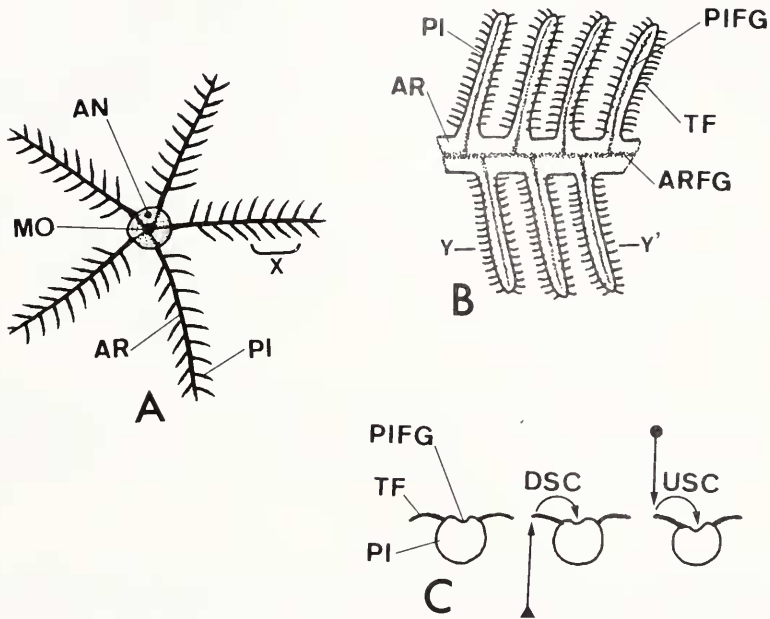


FIGURE 1. (A) Diagram of a crinoid showing the oral (mouth-bearing) side of the body. The mouth and anus open on the central disc from which the arms radiate. Each arm (usually more numerous than the 5 shown here) is fringed on either side by short side branches called pinnules. (B) Enlargement of the region opposite bracket x in Figure 1A. The arm food groove and pinnular food grooves run along the oral side of the arm and pinnules, respectively. Each pinnule is fringed by tube feet. (C) Cross section of three adjacent pinnules cut through plane y-y' in Figure 1B. The pinnular food grooves are on the oral side of the body, which is depicted facing upward. Downstream capture is diagrammed for the triangular particle, and upstream capture is diagrammed for the circular particle. Abbreviations: AN = anus, AR = arm, ARFG = arm food groove, DSC = downstream capture, MO = mouth, PI = pinnule, PIFG = pinnular food groove, TF = tube foot, USC = upstream capture.

strates that under surge conditions *O. serripinna* can alternate between upstream and downstream capture and (2) compares the efficiencies of these two processes.

The crinoid filter is diagrammed in Figure 1A,B. Approaching particles adhere to the adhesive tube feet, which rapidly bend and transfer the particles into the food grooves for transport to the mouth. The gut openings and food grooves are situated on the oral side of the body (*i.e.*, the side on which the mouth opens), which faces downcurrent during downstream capture. This behavior has been studied in detail for *O. serripinna* by Holland *et al.* (1986) and by Leonard *et al.* (1987). Downstream capture and upstream capture are shown diagrammatically in Figure 1C.

#### MATERIALS AND METHODS

We studied a feather star, *Oligometra serripinna*, living on sea fans at a depth of 10 m at North Reef, Lizard Island (14°38'S; 145°28'E), Great Barrier Reef, Australia. Current speed and direction in the microhabitat of *O. serripinna* were determined from underwater video recordings of a dye trail released by the non-motorized dye injector described by Colman *et al.* (1984). The study site and orientation of the injector relative to the crinoid are described by Leonard *et al.* (1987). We analyzed

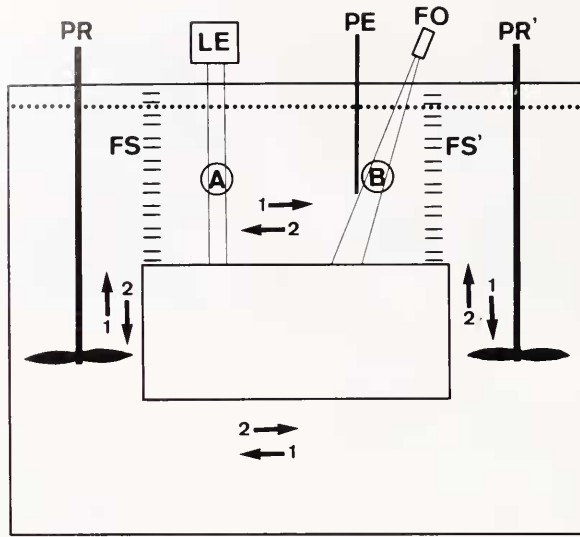


FIGURE 2. Diagram of 11-liter flume (45 cm long) for producing surging flow; the water level is indicated by the dotted line. To obtain flow in the predominant direction (indicated by arrows labeled 1), one propeller (=PR) is turned clockwise and the other (=PR') is turned counterclockwise for 6 s. To obtain flow in the reverse direction (indicated by arrows labeled 2), the action of each propeller is reversed for 2 s. At either end of the working section of the flume, there is a flow straightener (=FS and FS'). A bright beam of light is focused into the flume from above with a lens (=LE). A first video system records the speed and direction of brine shrimp cysts visualized in side view at the position marked by the circled A. An open mesh perch (shown in side view, =PE) supports the crinoid (not illustrated), which is illuminated with fiber optics (=FO). A second video system records the upstream and downstream captures in side view at the position marked by the circled B.

100 s of a recording made near slack tide at about 8:15 h on 16 August 1986. During every third of a second (*i.e.*, over 10 consecutive video frames), the speed and direction of the current was measured from the movement of irregularities in the dye stream. The predominant current toward the east-northeast was recorded as positive, and reversed current toward the west-southwest was recorded as negative.

The surge in the field was approximated in the laboratory in an 11-liter flume (Leonard *et al.*, 1987) to which an additional propeller and flow straightener had been added (Fig. 2). The two propellers were turned by a reversible, adjustable speed motor. One propeller turned clockwise and the other turned counterclockwise for 6 s to produce a *predominant flow* of approximately 5 cm/s. The action of the two propellers was then quickly reversed to produce a *reverse flow* for 2 s before the predominant flow was re-established and the cycle repeated.

The surge experiment in the flume was performed at 25°C, the approximate temperature in the field at the time. A specimen of *Oligometra serripinna* was allowed to attach to an open mesh perch with the food grooves facing downstream relative to the predominant current direction. Brine shrimp cysts that had been soaked in seawater for 8 h were then added to the flume. The concentration and speed of the cysts (and thereby the current speed) were measured as they passed through a segment of a light beam 2 cm in diameter and 1.8 cm from top to bottom (at position A in Fig. 2). The passing cysts were recorded in side view with a video system (Leonard *et al.*, 1987). A 100-s interval on the tape was quantified. Current speed was determined from the distance travelled by cysts over three consecutive video frames (*i.e.*, over an

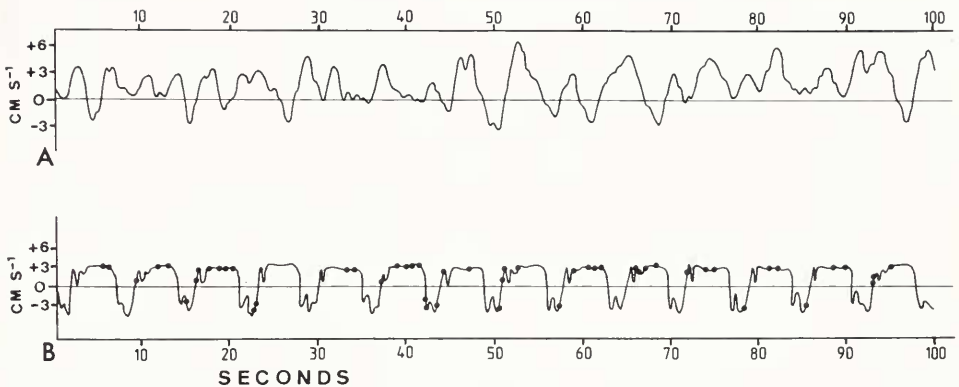


FIGURE 3. (A) Fluctuations in current velocity and direction (positive values are toward the east-northeast, and negative values are toward the west-southwest) in the microhabitat of *Oligometra serripinna*. (B) Fluctuations in current velocity and direction in a laboratory flume with surging flow (positive values are in the predominant direction, and negative values are for the relatively brief intervals of reversed flow). Each filled circle marks a point in the flow cycle where a brine shrimp cyst was captured.

interval of 0.1 s). Motion in the predominant direction was recorded as positive, and motion in the reverse direction was recorded as negative. During the same 100-s interval, one third of a single *O. serripinna* arm, with 20 pinnules (10 on each side), was recorded with a second video system, a duplicate of the first. The arm was recorded (at position B in Fig. 2) in side view a few degrees off the perpendicular to provide a foreshortened view of the pinnules on either side.

## RESULTS AND DISCUSSION

Figure 3A plots fluctuations in current speed and direction near slack tide in the microhabitat of *Oligometra serripinna*. During the 100-s period, there were 10 conspicuous reversals in current direction, most "negative flow" periods lasted about 2 s and reached speeds of approximately 3 cm/s.

The results of the laboratory flume surge experiment are shown in Figure 3B, which places cyst capture in the context of fluctuations in current speed and direction. During the 100-s period, 41 cysts were captured during the cumulative 70 s that flow was in the predominant direction (*i.e.*, downstream captures), and 10 cysts were captured during the cumulative 30 s that flow was in the reverse direction (*i.e.*, upstream captures). The video recordings showed that all the food grooves faced directly upstream throughout each current reversal. Thus, upstream capture was unequivocal.

The capture efficiencies during downstream and upstream capture, respectively, were calculated by counting the cysts crossing the light beam during the 70 s of predominant flow and during the 30 s of reverse flow. Each count was divided by the recorded area of the light beam normal to the flow (3.8 cm<sup>2</sup>) and multiplied by the recorded area of the arm normal to the flow (1.2 cm<sup>2</sup>). This gave the number of cysts approaching the recorded part of the crinoid's filter as 252 and 125 during predominant and reversed current flow, respectively. The capture efficiency (percentage of captures normalized to approaches) was 16.2% during downstream feeding and 8.0% during upstream feeding. We do not know why upstream capture was markedly less efficient than downstream capture. An explanation of this difference would probably



require a detailed knowledge of flow through the gaps in the filter and the thickness of the boundary layers around the tube feet and pinnules.

The distinction between upstream capturers and downstream capturers appears to be useful for suspension feeders that actively pump water past their filters in a single direction. However, this distinction may not apply for passive suspension feeders, which depend on exogenous currents to bring particles to their filters. For example, Patterson's (1984) work indicates that a given polyp of an octocoral can engage in either upstream or downstream capture depending on the strength and direction of the exogenous current. Moreover, the present study is the first clear demonstration that at least some crinoids can augment their usual downstream capture with upstream capture.

In the field, *Oligometra serripinna* probably obtains only a small proportion of its food by upstream capture because there are no flow reversals during most of the tidal cycle (Leonard *et al.*, 1987) and upstream capture is markedly less efficient than downstream capture. Even so, it is possible that upstream capture may be relatively important in some other crinoid species—especially those living within the infrastructure of reefs where slow, meandering flows predominate.

#### ACKNOWLEDGMENTS

This work was supported by NSF grants to N. D. Holland (OCE84-00671) and to J. R. Strickler (OCE84-16261). We are deeply indebted to the administration and staff of the Lizard Island Research Station, Queensland, Australia, for their hospitality and assistance. Our manuscript was constructively criticized by L. Z. Holland.

#### LITERATURE CITED

- BYRNE, M., AND A. R. FONTAINE. 1981. The feeding behaviour of *Florometra serripinna* (Echinodermata: Crinoidea), *Can. J. Zool.* **59**: 11–18.
- COLMAN, R. S., H. C. CRENSHAW, D. L. MEYER, AND J. R. STRICKLER. 1984. A non-motorized dye injector for visualization of flow *in situ* and its use with coral reef crinoids. *Mar. Biol.* **83**: 125–128.
- HOLLAND, N. D., J. R. STRICKLER, AND A. B. LEONARD. 1986. Particle interception, transport and rejection by the feather star *Oligometra serripinna* (Echinodermata: Crinoidea), studied by frame analysis of videotapes. *Mar. Biol.* **93**: 111–126.
- LA TOUCHE, R. W. 1978. The feeding behaviour of the featherstar *Antedon bifida* (Echinodermata: Crinoidea). *J. Mar. Biol. Ass. U. K.* **58**: 877–890.
- LEONARD, A. B., J. R. STRICKLER, AND N. D. HOLLAND. 1987. Effects of current speed on filtration during suspension feeding in *Oligometra serripinna* (Echinodermata: Crinoidea). *Mar. Biol.* (in press.)
- MAGNUS, D. B. E. 1967. Ecological and ethological studies and experiments on echinoderms of the Red Sea. *Stud. Trop. Oceanogr.* **5**: 635–664.
- MEYER, D. L. 1979. Length and spacing of the tube feet in crinoids (Echinodermata) and their role in suspension-feeding. *Mar. Biol.* **51**: 361–369.
- MEYER, D. L. 1982. Food and feeding mechanisms: Crinozoa. Pp. 25–42 in *Echinoderm Nutrition*, M. Jangoux and J. M. Lawrence, eds. Balkema, Rotterdam.
- PATTERSON, M. R. 1984. Patterns of whole colony prey capture in the octocoral, *Alcyonium siderium*. *Biol. Bull.* **167**: 613–629.